

# A revision of the genus *Mitella* with a discussion of geographical distribution and relationships.

By

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With 9 fig. and 4 chart. (Table VIII.)

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## Part. I, Introductory.

The genus *Mitella* has experienced at the hands of systematic workers a degree of splitting up into petty genera which is wholly inconsistent with its well-marked generic characters and which does violence to the lines of genetic development running through the group. The divisions in all cases have been made upon one or two characters which are obvious and artificial rather than fundamental, and the resulting genera, although easy enough to recognize, are wholly artificial and arbitrary.

It has always been one of the common weaknesses of taxonomic work to employ single characters and greatly to overestimate their importance in distinguishing groups or constructing schemes of classification. The evil results of such procedure are well illustrated in the breaking up of the genus under discussion. Another pernicious practice is that pursued in many floras of proceeding to slash and dismember families and genera on the basis of only the material represented within the geographical limits of the particular flora, when the probabilities are that many, yes often a large proportion, of the genera and species occur only outside such area.

It would be interesting in this connection to trace the history of the genus *Mitella* and see what vicissitudes it has gone through, but lack of space prevents such details. Since the latest monographic work on the genus by P. A. RYDBERG in the North American Flora, Volume 22, Part 2, pages 94—96, 1905, — embodies all the important divisions that have at different times been suggested, it will be sufficient for our purpose to refer in detail only to this latest work.

In his treatment of the group. Mr. RYDBERG carries the splitting-up tendency to the greatest extreme. Every section of the old genus, except one, is raised to generic rank, varieties are made into species and many new species are described. Where ENGLER in 1890 recognized one genus and seven species, including one from Japan, this latest work recognizes

four genera and eighteen species exclusive of the Japanese ones. As this latest work on *Mitella* adopts all the genera that taxonomists have at different times proposed for the group, so also it utilizes in a similar artificial manner the characters that have been employed for their separation. An enumeration of these characters and the manner in which they are used as the basis of classification will be taken up at this point before proceeding to what we consider a more natural and consistent arrangement.

The number and disposition of the stamens has been taken as of first importance in the division and splitting-up of the genus. As the stamens are either 40 or 5 in number it allows of three divisions being made; one division with 40 stamens, one with 5 stamens opposite the petals, and one with 5 opposite the sepals. When it is borne in mind that plants like *M. nuda* and *M. caulescens*, which in every other way show the closest possible natural relation, would be separated from each other by this scheme, it is at once seen that such a character as stamen number has no more significance here in defining affinities than in the Linnaean artificial system.

Furthermore, it often happens, as pointed out by HOOKER<sup>1)</sup> and PIPER<sup>2)</sup>, that one or more stamens in the 5-stamen groups are transformed into staminodia, a fact which further shows the inconstancy of stamen characters in this genus.

The extent of fusion between the pistil and the axis has been considered as a character of sectional or generic merit. In two of the most closely related species of the genus, *M. nuda* and *M. caulescens*, this character does not hold good. In the former the ovary is free from the axis to the base, whereas in the latter the ovary is half inferior. In the section *Eumitella* the placentae have been regarded as more basal than in the others. This is either an error in observation or a failure to recognize the fact that modifications take place in the ripening fruit which affect the apparent position of these structures. The placentae are in all cases parietal but the ovary, varying in the extent of its fusion with the axis, behaves differently in ripening into the capsule. Where it is free or only slightly fused with the axis the enlargement of the capsule is mainly above the placentae, making them appear relatively basal in the fruit, and on the other hand, where it is deeply sunk in the axis, the growth of the capsule is more basal so that the ripening fruit evaginates more or less completely causing the placentae to appear higher placed.

*Eumitella* has also been characterized as having larger and fewer ovules, but as this applies really only to *M. diphylla* it cannot be considered of any value in holding *M. diphylla* and *M. nuda* together as distinct from the others.

1) HOOKER, W. J., Fl. Bor. Am. vol. 4 p. 241. 1840.

2) PIPER, C. V., Erythea, vol. 7 p. 163. 1899.

In attempting to rehabilitate the old genus as HOOKER, GRAY and ENGLER progressively adopted it, and in the hope of avoiding as far as possible the common causes of error referred to above, the present work is based in the first place upon the study of extensive material from the whole geographical area of the genus and, in the second place, upon the proposition that a single morphological character is insufficient ground upon which to base generic or even sectional concepts.

In seeking for a better basis upon which to lay down the lines of genetic development in the genus, it was hoped that anatomical structures of value in classification would be found. Nothing of importance, however, has been revealed aside from bringing to light the close relationship existing between the species *M. nuda* and *M. caulescens*. — It should, however, be added that herbarium material proves unsatisfactory for close anatomical work and that ample fresh material might give additional results. — In a similar manner it has been shown that purely vegetative characters are wholly inadequate and of value only in differentiating the species.

It is therefore clear that the floral characters are the only ones that can be relied upon. A comparative morphological study of the various organs of the flowers of all the species reveals the fact that in the artificial and arbitrary division of the genus based upon position and number of stamens, morphological structures of far greater importance for classification purposes have been ignored. Briefly stated, these are found to be: (a) shape of the floral axis, (b) form and venation of the sepals, (c) structure and division of the petals and (d) form of the anthers.

An examination of figures 4—8, following the systematic part of this work, will show at once a remarkable agreement in the ground-plan of these structures which seems quite significant, and one that cannot be ignored in dealing with affinities. It is on the basis of a combination of these characters that we present the following new alignment of species and reduction of the number of sections. Their merit will be argued in the discussion on relationship in Part III.

### *Mitella* (Tourn.) L.<sup>4</sup>.

*Mitella* (Tourn.) L. Gen. Ed. 4. 434. 1737. — *Drummondia* DC. Prod. IV. 49. 1830. — *Pectiantia* Rafin. Fl. Tell. II. 72. 1836. — *Oxomelis* Rafin. II. 73. 1836. — *Mitellopsis* Meisner, Pl. Vasc. Gen. 400. 1838. — *Mitelalstra* (T et G) Howell, Fl. NW. Am. 204. 1898.

Axis cup-shaped, saucer-shaped, campanulate or turbinate, more or less united with the ovary. Sepals 5, oblong, ovate or triangular, valvate in the bud. Petals 5, pinnately cleft, pinnately divided, trifid or entire

4) The name is derived from the Greek word *μῖτρα*, meaning a headband or a turban. It was applied by TOURNEFORT on account of the resemblance of the dehiscing capsule to the mitre or bishops cap.



white, greenish yellow, violet-tinged or purple. Stamens 10 or 5, when only 5 either opposite the sepals or opposite the petals; filaments short or sometimes exceeding the anthers; anthers oblong, cordate or reniform. Disk lobed or entire, more or less lining the hollow axis or covering the ovary. Carpels 2, united into a 4-celled pistil with 2 parietal placentae; styles 2, distinct, short and thick or slender and tapering into the stigmas; stigmas rounded, crescent-shaped or 2—4-lobed; ovules numerous. Capsule 2-beaked, dehiscing early into a mitre- or cup-shaped fruit. Seeds numerous, smooth and shining or black spotted. Perennial herbs, by creeping or ascending rhizomes, in some species producing leafy runners; flowering stems lateral, naked or with 1—3 alternate or opposite leaves. Leaves alternate on the rhizome, long-petioled, rounded, cordate, or reniform, variously toothed or lobed. Inflorescence racemose, with simple, spike-like racemes, or often with several 2-flowered cymes towards the base.

A genus of about 12 species of the north temperate and boreal regions of North America and Asia.

### Key to the Sections.

- A. Axis cup-shaped, campanulate or turbinate, longer than broad; sepals oblong or ovate, erect or only slightly spreading at the tips; petals white or violet-tinged, pinnately cleft with ascending divisions, palmately 3—5-fid or entire; anthers oblong; stigmas capitate or obscurely crescent-shaped . . . Sect. I. *Eumitella*
- B. Axis saucer-shaped or strongly flattened, much broader than long; sepals triangular, strongly spreading or reflexed; petals greenish-yellow or purple, pectinate-pinnatifid, with the divisions spreading nearly at right angles; anthers cordate or reniform; stigmas pointed or strongly 2—4-lobed . . . . . Sect. II. *Mitellastra*

### Analytical key to the species.

#### Sect. I. *Eumitella*

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|--|---------------------------|
| 1. Stamens 10, petals pinnately cleft, 2 cauline leaves opposite   | 4. <i>M. diphylla</i>     |
| 2. Stamens 5, opposite the sepals, petals palmately 3—5-cleft or entire  |                           |
| a. Leaves rounded, ovate, cordate or reniform, toothed or crenate, all basal   |                           |
| (1) Petals with slender filiform limb, trifid above the middle with slender branches, or entire, mid-vein of sepals unbranched, flowers secund . . . . . | 2. <i>M. stauropetala</i> |
| (2) Petals with broad limb, cuneate and trifid or oblanceolate and entire, mid-vein of sepals more or less branched, flowers not secund . . . . .        | 3. <i>M. trifida</i>      |
| b. Leaves cordate-triangular, angularly lobed, petals palmately 3—5-cleft, one cauline leaf . . . . .  | 4. <i>M. diversifolia</i> |

#### Sect. II. *Mitellastra*

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|--|-------------------|
| 1. Stamens 10, ovary free from the axis to the base. . . . . | 5. <i>M. nuda</i> |
| 2. Stamens 5, ovary more or less united with the axis        |                   |

## a. Stamens opposite the sepals

- (1) Expanded calyx more than 5 mm. across, styles tapering, ascending, stigmas entire, 4—3 cauline leaves . . . . 6. *M. caulescens*
- (2) Expanded calyx less than 5 mm. across, styles thickened upward, stigmas 2-lobed, leaves all basal
- (a) Leaves broadly cordate to reniform, broader than long, nearly smooth above, petals with 5—8 divisions 7. *M. Breweri*.
- (b) Leaves oval to oval-oblong, longer than broad, prominently white-hirsute above, petals with 3—5 divisions . . . . . 8. *M. ovalis*

## b. Stamens opposite the petals

- (1) Petals greenish-yellow, without glands on the dorsal side, disk covering the ovary, sepals strongly reflexed . . . 9. *M. pentandra*
- (2) Petals purplish, dotted with conspicuous glands on the dorsal side, disk not covering the ovary, sepals spreading or reflexed only at the tip
- (a) Stamens inserted on the angular disk, styles slender, stigmas not lobed, scapes few-flowered . . . . . 10. *M. pauciflora*
- (b) Stamens inserted at the base of the petals, styles thick and short, stigmas 2—4-lobed, scapes secundly many-flowered
- x. Leaves glandular pubescent on both sides and on the petioles, petals with 5—7 divisions . . . . 11. *M. japonica*
- y. Leaves glabrous below and on the petioles, petals with 3 divisions . . . . . 12. *M. acerina*.

1. *Mitella diphylla* L. Sp. Pl. 406. 1753. — Rhizome creeping, more or less branching; flowering stems slender, erect, 1.2—4.5 dm. high, bifoliate above the middle, pubescent with scattered hairs below the cauline leaves, glandular-puberulent above; basal leaves cordate, 3—5-lobed, crenate-dentate, thin, thinly pubescent above, prominently pubescent, especially along the veins beneath, with long, strigose hairs, 3—9 cm. long, 2.5—8 cm. broad; petiole slender prominently retrorse-hairy, 4—17 cm. long; cauline leaves 2, opposite, sessile or nearly so, unequal, prominently 3-lobed, middle lobe much elongated, 4—7 cm. long; raceme 5—20-flowered, 6—20 cm. long, glandular-puberulent; bracts minute, broadly triangular; pedicels 1—2 mm. long; flowers 5—6.5 mm. broad in anthesis, white; sepals oblong, whitish; petals pinnately cleft, spreading; anthers oblong, filaments very short; disk not lobed; ovary free nearly to the base, glandular puberulent, styles very short, stigmas crescent-shaped; capsule ovoid, dehiscing early into a mitre-shaped fruit.

In rich deciduous forests. Distributed from New Hampshire and Vermont northward in Quebec to about latitude 47° N, and west to central Minnesota about the same latitude. It extends south into western North Carolina and eastern Tennessee and westward in its southern range to the middle of Missouri.

The species is very variable as to foliage. The greatest variation is found in the cauline leaves which are either sessile and practically oppo-

site or more or less petioled and tending to become alternate, and with distinct stipules 2—3 mm. long. The following forms are among the most noteworthy:

Forma **oppositifolia** (Rydb.). — *M. oppositifolia* Rydb. N. Am. Fl. 22; 2. 91. 1905. — A plant with petioled stem leaves, said also to differ in sepals and petals from the species.

Collected in Massachusetts by A. S. KINNEY.

Forma **triphylla**. A form bearing two nearly opposite short-petioled leaves and a smaller sessile one higher up on the stem.

Collected at Milaca, Minnesota, 1892, by E. P. SHELDON (2789).

2. **Mitella stauropetala** Piper, Erythea Vol. 7. 461. 1899. — *Oxomelis stauropetala* (Piper) Rydb. N. Am. Fl. 22. 2. 95. 1905. — Rhizomes creeping, stolon-like, with conspicuous scale-leaves; flowering stems 4—6, erect, slender, with few scarious fimbriate bracts, thinly pubescent below, glandular-puberulent above, 3—5 dm. high; leaves cordate, orbicular, or reniform, mostly obscurely 5—7-lobed, more or less distinctly crenate, thinly hirsute with white or reddish hairs on both sides, 3—9 cm. long, 3—8 cm. broad; petioles stoutish, retrorsely-hirsute especially toward the upper end, 5—15 cm. long; racemes secund, 10—35-flowered, 6—20 cm long, glandular-puberulent; bracts lanceolate, variously toothed or lacerate; pedicels about 4 mm. long; flowers white or violet-tinged, 6—7 mm. broad, in anthesis, 5—6 mm. long; axis turbinate or campanulate; sepals oblong to obovate, nearly erect, about 2 mm. long, mid-vein unbranched; petals white, slender, 3-parted above the middle into narrow filiform divisions, spreading, about 4 mm. long; anthers large, oblong, nearly sessile; ovary fully half united with the axis, styles thick, glandular-puberulent, stigmas capitate; capsule depressed-ovoid, dehiscing cup-shaped; seeds numerous, black and shiny.

Common in the wooded regions of northern Idaho. Extends into northwestern Montana, northeastern Oregon, and southeastward to southern Idaho, passing into the following variety in Utah. Wyoming and Colorado:

Var. **stenopetala** (Piper) n. comb. — *M. stenopetala* Piper, Erythea Vol. 7. 461. 1899. — *Oxomelis stenopetala* (Piper) Rydb. N. Am. Fl. 22. 2. 96. 1905. — *M. stenopetala* var. *Parryi* Piper, Erythea 7. 462. 1899. — *Oxomelis Parryi* (Piper) Rydb. N. Am. Fl. 22. 2. 96. 1905. — More slender than the species, stems sparingly pubescent and puberulent; leaves sometimes more conspicuously crenately-lobed (not in the type), nearly glabrous on both sides; petioles with scattered retrorse hairs above; racemes 10—25-flowered, 5—10 cm. long; flowers very variable in size but smaller than in the species; petals 3-parted above the middle into narrow divisions or entire.

In moist springy places from Yellowstone National Park and northern



Wyoming to southwestern Colorado; ranging east and west from Laramie, Wyoming, to Salt Lake, Utah.

This variety is the southward extension of the species, the ranges of the two overlapping in southeastern and eastern Idaho. It is very variable with the age and size of the individual plants and with the habitat. Old sturdy individuals produce larger leaves and flowers than young plants, and those growing in shady situations have very large thin leaves as well as tall flowering stems. The petals are extremely variable, ranging from deeply 3-parted to those that are unequally 3—2-parted and entire. We regard *M. stenopetala* var. *Parryi* Piper as nothing but a young or small individual of var. *stenopetala*.

3. *Mitella trifida* Graham, Edinb. New Phil. Journ. 185. 1829. — *Oxomelis varians* Rafin. Fl. Tell. 2. 75. 1836. — *Mitelloides Hookeri* Meisn. Pl. Vasc. Gen. 100. 1838. — *Lithophragma nudicaulis* Nutt. Mss. in T. et G. Fl. N. Am. 4. 587. 1840. — *Mitelloides trifida* Walp. Rep. 2. 370. 1843. — *Mitella anomala* Piper, Erythea 7. 162. 1899. — *Oxomelis trifida* (Graham) Rydb. N. Am. Fl. 22. 2. 95. 1906. — *Oxomelis pacifica* Rydb. N. Am. Fl. 22. 2. 95. 1905. — Rhizome ascending, becoming quite thick in old plants; flowering stems 4-several, slender, erect, 4.5—4.5 dm. high, glandular-pubescent, bearing 4 or 2 bracts and very rarely a single leaf near the base; leaves cordate to orbicular and reniform, faintly crenate or more or less deeply crenate-lobed, pubescent with scattered stiff white hairs above, nearly glabrous below, 2—8 cm. long, 2—7 cm. wide; petioles prominently retrose-hairy especially above the middle; racemes 7—20 flowered, 3—12 cm. long, puberulent; bracts lanceolate, lacerate-toothed; pedicels very short; flowers 2—4 mm. broad in anthesis, 3—5 mm. long; axis campanulate; sepals oblong, whitish to violet-tinged, 4—4.5 mm. long, midvein usually branched; petals cuneate and trifid, 2—2.6 mm. long, white or violet-tinged; anthers ovate-oblong, filament very short; ovary half united with the axis, styles thick, glandular-puberulent, stigmas capitate; capsule depressed-ovoid, dehiscing broadly cup-shaped; seeds numerous, black and shiny.

A polymorphous species, widely distributed in the Rocky, Selkirk, Cascade and Olympic Mountains. In the Rocky Mountains it extends, with the varieties and forms included, from southern Montana to about latitude 60 degrees north; in the Cascades from Northern California to about latitude 54° N.

The following variety seems fairly wellmarked:

Var. *violacea* (Rydb.) Rosend. Englers Bot. Jahrb. 37. 2. 83. 1905. — *M. violacea* Rydb. Bull. Torr. Bot. Club. 24. 248. 1897. — *Oxomelis violacea* Rydb. N. Am. Fl. 22. 2. 95. 1905. — Petals oblanceolate, slightly exceeding the sepals, entire or slightly and unequally toothed, sepals and petals often violet tinged.

In the Rocky Mountains from southern Montana to about latitude 52° N.

Forma *mierantha* — *M. mierantha* Piper, Erythea 7: 462. 1899. — *Oxomelis mierantha* (Piper) Rydb. N. Am. Fl. 22: 2. 96. 1905. — Flowers small, petals entire, 3-veined; stems flexuous; leaves cordate, some of them large and obscurely lobed, others of typical shape.

Fort Colville, Washington, collected by S. WATSON, Sept. 29. 1880.

Note: This plant appears somewhat abnormal in its flowers, probably due to the fact that it was blooming so late in the year. The foliage is nearly identical with that of specimens from Mt. Stewart, Wash. collected by SANDBERG and LEIBERG in 1893. In the examination of a very large number of specimens we have found nothing to correspond with the type and therefore feel constrained to regard it merely as a curious or aberrant form. *M. anomala* Piper appears to be nothing but an individual plant in which the petals are wanting and some of the stamens modified into staminodia. We do not see how it ever could have been regarded as a species for even the type is a poor specimen with a few flowers mostly in fruit.

Note: *Oxomelis pacifica* Rydb. is in our opinion nothing but larger flowered forms of *M. trifida* Graham and comes closer to being the typical species as originally described and figured by GRAHAM and later by HOOKER in the Fl. Bor. Am. than *Oxomelis trifida* (Graham) Rydb. of the N. Am. Fl. It should be borne in mind that the species was originally described from plants grown in the Edinburgh Botanic gardens from seeds brought from the northern Rocky Mts. and that in a climate like that of Edinburgh more robust and larger flowered individuals, more like those of the Cascade and Olympic Mountains, would likely develop than in the high and dry northern Rockies.

4. *Mitella diversifolia* Greene, Pittonia 1: 32. 1887. — *M. diversifolia* Piper, Erythea 7: 462. 1899. — *Oxomelis diversifolia* (Greene) Rydb. N. Am. Fl. 22. 2. 94. 1905. — Rhizome ascending or erect, thickened; flowering stems several, stoutish towards the base, 2—4 dm. high, usually bearing a single long-petioled leaf some distance from the base, glandular-puberulent throughout; basal leaves triangular-cordate, with a deep sinus at the base, more or less angularly lobed, irregularly crenate, glandular-puberulent on both sides, with a few strigose hairs on the upper surface, 4—9 cm. long, 3—7 cm. broad; petioles 3—10 cm. long, retrosely hairy; racemes slender, 12—35 flowered, 6—15 cm. long, lower flowers remote; flowers 3—4 mm. long, about 2 mm broad, nearly sessile; sepals erect, oblong triangular, strongly mucronate-pointed, very glandular-puberulent; petals cuneate, palmately 3—5-cleft, not spreading, about 2 mm. long; stamens with oblong anthers and very short filaments; ovary more than half fused with the turbinate axis, styles very short and thick, stigmas capitate, glandular-puberulent; capsule ovoid projecting very little beyond the sepals when dehiscing; seeds black, very numerous.

A distinct species; occurring in wet places in the mountains from northern California to southern Washington.

5. *Mitella nuda* L. Sp. Pl. 406. 1753. — *M. scapo-nudo* Gmel. Fl. Siber. 4: 175. 1769. — *Tiarella unifolia* Retz. Obs. 3: 30. 1783. —



*M. reniformis* Lam. Tab. Encyc. 2: 495. 1793. — *M. cordifolia* Lam. III. t. 373. 2. — Rhizome slender, creeping, spreading freely by runners; flowering stems very slender, erect, 5—18 cm. high, glandular-pubescent throughout, naked or with 1—3 short-petioled, cauline leaves; basal leaves cordate to reniform, crenately lobed and shallow-toothed, pubescent with white strigose hairs above, very sparsely pubescent beneath, 1—4 cm long, 1—4.5 cm. wide, cauline leaves triangular-cordate, about 3-lobed; petioles very slender, more or less retrorsely hairy, 1—10 cm. long; raceme 3—10-flowered, 3—11 cm. long; bracts lanceolate, mostly obsolete in the last flowers pedicels 2—5 mm. long, glandular pubescent, bracteoles minute; flowers 8—12 mm. broad in anthesis, greenish yellow; axis strongly flattened; sepals triangular, spreading, 1.3—1.6 mm long; petals yellowish green 3—3.5 mm. long, pectinate-pinnatifid, divisions very slender; stamens erect, filaments slender, longer than the cordate anthers; disk prominently lobed; ovary free from the axis to the base, glandular-puberulent, styles tapering, stigmas pointed; capsule ovoid, flattened, dehiscing into a shallow cup-shaped fruit.

In deep moist woods and boggy places, mostly in conifereous forests. Distributed from Newfoundland through Labrador and to the Arctic Sea westward to the Mackenzie River; it extends south into Connecticut, Pennsylvania, southern Michigan and to latitude 45° N. in eastern Minnesota. In the Rocky Mountains it reaches the southern limit in northern Montana. In the old world it is distributed from northeastern Asia as far west as the Yenisei River and probably as far south as the 59th parallel.

The most important variations of the species are:

Forma **prostrata**. — *Mitella prostrata* Michx. Fl. Bor. Am. 4: 270. 1803. — A form in which the runner ends in an upright flowering shoot bearing several small angularly-lobed leaves.

Collected near Lake Champlain by Michaux, and near Gaylordsville, Massachusetts, by Mr. C. K. AVERILL.

Forma **intermedia**. — *M. intermedia* Bruhin. N. Am. Fl. 22: 2. 92. 1905. — *M. diphylla* L. forma *intermedia* (Rydb.) Rosend. Englers Bot. Jahrb. 37: 2. 82. 1905. — An interesting form with all the essential characters of *M. nuda* except that the flowers are reported by the collector as white and the petals are intermediate in form between those of *M. nuda* and *M. diphylla*. It has the same kind of calyx, pistil and stamens as *M. nuda*, and the disk is similarly lobed. The cauline leaves are inclined to be slightly broader and larger than the similar ones of *M. nuda*.

Only one collection of this form is known and this was made by the Rev. Th. A. BRUHIN in Manitowoc County, Wisconsin, June 7th, 1876. Of this collection one sheet is in the Gray Herbarium and the other in the U. S. National Herbarium. According to the collector the plants were found growing together with *M. nuda*. It has the appearance of being

a natural hybrid between *M. nuda* and *M. diphylla*, and for that reason it seems hardly necessary to regard it as of higher rank than here accorded to it.

6. *Mitella caulescens* Nutt. T. et G. Fl. N. Am. 4: 586. 1840. — *Mitellastra caulescens* (Nutt.) Howell, Fl. N. W. Am. 201. 1898. — Rhizomes creeping or ascending, producing long, slender, leafy runners; flowering stems erect, slender, 1.2—3.5 dm. high, bearing 1—3 petioled leaves, thinly glandular-pubescent or hirsute; leaves round-cordata to reniform, conspicuously 3—5-lobed, crenate or crenate-dentate, thin, sparsely hirsute on both sides, becoming nearly glabrous in age, 2—7 cm. long, 2—7 cm. wide; cauline leaves and leaves of the runners smaller; petioles slender sparsely retrorse-hirsute, 4—12 cm. long; raceme 5—10-flowered, 3—10 cm. long, glandular-puberulent; bracts minute, triangular, glandular-toothed; pedicels slender, deflexed in bud, 2—8 mm long; flowers yellowish green, 9—12 mm. across in anthesis; sepals ovate triangular, spreading, 1.8—2 mm. long; petals yellowish green, often purplish towards the base, pectinate-pinnatifid with slender divisions, minutely glandular, 3—4 mm. long; stamens 1.2—1.7 mm long, filaments slender, often purple, anthers cordate; disk lining the hollow axis; ovary nearly half-inferior, puberulent, styles slender, divergent, stigmas simple, rounded, ovules very small and numerous; capsule globose-ovoid, prominently 2-beaker; seeds large, black and shiny.

In shady woods and moist places mostly at altitudes of 2,000 to 4,000 feet, from southern British Columbia and Vancouver Island to northern California, and from northwestern Montana and northern Idaho south to the middle of western Idaho.

7. *Mitella Breweri* A Gray, Proc. Am. Acad. 6: 533. 1865. — *Pectiantia Breweri* (A. Gray) Rydb. N. Am. Fl. 22: 2. 93. 1905. — Rhizome slender, creeping, sometimes producing stolon-like offsets; flowering stems very slender, naked, sparsely glandular-pubescent, becoming glabrous in age, 1—2.2 dm. high; leaves all basal, orbicular to reniform, with a broad sinus at the base, and with many rounded lobes, incisely and doubly crenate, thin, with a few scattered hairs on both sides, becoming glabrous, 2.5—7 cm. long, 3—8 cm. broad; petioles stoutish, shaggy, reddish-hirsute, becoming quite glabrous in age, 4—12 cm. long; inflorescence a simple raceme or more often racemose with numerous 2-flowered cymes, glandular-puberulent, 5—10 cm. long, 10—25-flowered; bracts obovate, glandular-fringed; pedicels 1—4 mm long with 2 minute bracteoles at the base; flowers greenish yellow, 7—9 mm. across in anthesis; axis saucer-shaped; sepals triangular, spreading, slightly reflexed at the tips, about 1 mm. long; petals pectinate-pinnatifid, 2—3 mm. long, the 5—7 lobes filiform; disk 5-lobed; stamens 5, opposite the sepals, very short, anthers cordate; ovary half inferior, styles strongly spreading, stigmas 2-lobed; capsule

ovoid, depressed, dehiscent early and evaginating in ripening; seeds black, shiny.

In damp woods and moist slopes in the mountains. Distributed from about latitude  $36^{\circ}$  N. in the high Sierra Nevada Mountains of California, northward into the Cascade Range to about latitude  $52^{\circ}$  N. It occurs also in the Coast Range in Chehalis County, Washington, and probably in the Olympic Mountains. In the Rockies, it is distributed from middle western Idaho, northwestern Montana, and northward in British Columbia to about latitude  $52^{\circ}$  N.

A number of geographical forms can be distinguished in this species, the most noteworthy being the following:

**Forma lobata.** — With very large prominently crenate-lobed, shallow-toothed leaves; inflorescence with numerous 2-flowered cymes and up to 45 flowers, pedicels very slender, wide-spreading and longer than in the typical species, flowers inclined to be smaller.

In Placer and Nevada Counties, California, in the region of Lake Tahoe and Donner Lake.

CHESTNUT and DREW, Glen Alpine. J. BURT DAVY, No. 3231. E. A. MCGREGOR, No. 97.

**Forma denticulata.** — Leaves obscurely crenate-lobed, minutely serrate or denticulate, thin and veiny, pedicels of the flowers short, not over 2 mm. long.

In the Canadian Rockies and Silkirk Mountain, British Columbia. F. K. BUTTERS and E. D. W. HOLWAY, No. 142, Prospectors Valley.

8. *Mitella ovalis* Greene, Pittonia 1: 32. 1837. — *M. Hallii* Howell, Erythraea 3: 35. 1895. — *Pectiantia ovalis* (Greene) Rydb. N. Am. Fl. 22: 2. 94. 1905. — Rhizome creeping, stolon-like, with prominent scale leaves; flowering stems erect, 1.5—3.5 dm. high, naked or with 1 or 2 brownish bracts, more or less hirsute with spreading hairs, leaves all basal, oval or oblong-ovate, with 5—9 rounded or crenate lobes, broadly crenate-toothed, upper surface pubescent with scattered, coarse, white hairs, hirsute along the veins beneath, 2.5—7 cm. long, 1.5—4.5 cm. broad; petioles stoutish, 5—11 cm. long, densely retrorse-hirsute with long rusty hairs: inflorescence racemose, but often with numerous 2-flowered cymes towards the base, glandular-puberulent, 10—35-flowered, 4—12 cm. long; pedicels about 1 mm. long, bracts minute, triangular; flowers greenish yellow, about 5 mm. broad in anthesis; axis flattened; sepals triangular, 1 mm. long, reflexed at the tips; petals pectinate-pinnatifid with 3—5 filiform divisions, 1.5—1.7 mm. long; stamens 5, opposite the sepals, very short, anthers cordate; ovary inferior, styles spreading, deflexed at the ends, stigmas 2-lobed, ovules few; capsule ovoid, dehiscent into a cup-shaped fruit; seeds few, black or brownish.



In moist or shady places in the coniferous forests of the coast country from northern California to Vancouver Island.

9. *Mitella pentandra* Hook. Bot. Mag. pl. 2933. 1829. — *Drummondia mitelloides* DC. Prod. 4: 50. 1830. — *Pectiantia mitelloides* Raf. Fl. Tell. 2: 72. 1836. — *Mitellopsis Drummondia* Meisn. Pl. Vacs. Gen. 100. 1836. — *Mitellopsis pentandra* Walp. Gep. 2: 370. 1840. — *Pectiantia pentandra* (Hook.) Rydb. N. Am. Fl. 22: 2. 93. 1905. — *Pectiantia latiflora* Rydb. N. Am. Fl. 22: 2. 93. 1905. — Rhizome creeping or ascending, sometimes stolon-like, becoming stout in old plants; scapes slender, erect, naked or with one or two scarious bracts or sometimes with a single, petioled leaf near the base, glabrous or with few, scattered, stiff hairs, and glandular puberulent, 1—4 dm. high; leaves cordate-ovate or sometimes nearly orbicular, crenately several-lobed, very sparsely hirsute with white hairs on both surfaces or quite glabrous, 2.5—7 cm. long, 2—6 cm. wide; petioles slender, 3—14 cm. long, sparingly retrorse-hirsute, or sometimes becoming quite glabrous in age; racemes simple or frequently with 2-flowered cymes, 3—12 cm. long; bracts deltoid to obovoid and bilobed, glandular fringed; pedicels 2—4 mm. long, glandular-puberulent, with two minute bracteoles at the base; flowers yellowish green, 6—9 mm. across in anthesis; axis saucer-shaped; sepals triangular, strongly reflexed, about 1 mm. long; petals yellowish green, spreading or slightly reflexed, 2—2.8 mm. long, pectinate-pinnatifid, with 7—10 divisions; stamens 5, very short, inserted at the base of the petals, anthers reniform; disk mostly purplish brown, nearly covering the ovary; ovary inferior, styles short and spreading, stigmas bilobed; capsule depressed-ovoid, evaginating in fruit; seeds numerous, black and shiny.

On banks of cold streams, in swamps and bogs in the mountains. Distributed from southern Colorado far north in the Rocky Mountains and from eastern middle California and western Nevada northward in the Sierra Nevada mountains into the Coast and Cascade Ranges northward to Alaska.

This widely distributed species is somewhat variable as to size and hairiness of leaf, length of petioles, etc. the following forms are noteworthy:

*Forma stolonifera.* — Producing leafy runners, leaves nearly orbicular, sometimes acutish, with a closed sinus at the base, crenately many-lobed, prominently hirsute on both sides and on the petioles, frequently with a single small cauline leaf; petioles longer than in the species; the second flower of the 2-flowered cymes often borne some distance up on the pedicel of the first flower.

In swamps, upper valley of the Nesqually, Mt. Ranier, C. D. ALLEN, No. 5. E. C. SMITH, Mt. Ranier, alt. 4000 ft. Aug. 1880. — with very coarsely-dentate leaves. These may be the same as *Pectiantia latiflora*

of P. A. RYDBERG. The flowers of this form do not, however, average any larger than the species.

**Forma maxima.** — Stems stout, 4—5 dm. high, leaves 8—10 cm. long, 7.5—9 cm. wide, coarsely crenate-lobed.

Selkirk Mountains, British Columbia, E. L. GREENE, Journey of 1890.

10. *Mitella pauciflora* Rosend. n. sp. — Rhizoma repens, stoloniferus, tandem crassiusculus. Folia radicalia, cordata, 2—8 cm. longa, 2—7 cm. lata, lobo medio obtuso aut acutiore, dentibus mucronatis bi-crenato-dentata, capillis supra albis sparsis hirsuta, inferne ad vena similiter hirsuta aut glabra; petioli crassiusculi, inferne vaginis stipularibus magnis fulvis instructi. Scapi aphylli, 9—22 cm. alti, sparsim hirsuti, primum adscendentes, flexuosi, tum in fructificatione erecti; racemi 3—6 cm. longi, floribus 4—7, bracteis late triangularibus integris, pedicellis 3—6 mm. longis, inferne minute bibracteolatis aut pedicello floris terminalis longiore et medio bibracteolato. Flores brunneo-purpurei aperti, 9—10 mm. lati, axe valde complanato, sepalis late triangularibus, supra reflexis bi-trifidis, petalis 4—4.5 mm. longis itemque latis, atropurpureis, partibus 7—9 angustis pectinatim pinnatifidis, partibus dorsalibus glanduloso-punctatis, disco valde 5-lobato, staminibus 5, ob petala in discum dimidio inter petala ac stylos insertis, filamentis brevissimis atque antheris reniformibus instructis; stylis ad 1 mm. longis, cylindraceis aut supra nonnihil tenuioribus, stigmata integra minuta ferentibus. Capsulae apertae crateriformes, paucis seminibus fulvis maculatis linealiter verrucosus instructae.

In moist places, from the central to the southern part of the Island Nippon. MINASAKA, May 10, 1904, SHINTARO ARIMATO, Type in Gray Herbarium. Hondo, MINASAKA, April 5, 1904. Chichibu, J. MATSUMURA, Sheet No. 139560 in U. S. Natl. Herb.

Note. This species is readily distinguished from *M. japonica* with which it has been confused by the less pointed leaves, few-flowered, flexuous, short scapes, larger flatter flowers, and especially by the stamens being borne on the large 5-lobed disk and by the small entire stigmas. It appears from a note following Maximowicz' description of *M. japonica*, that he may have had this species before him in distinguishing two forms of the species. The two characters which he refers to, namely the shorter terminal lobe of the leaf and shorter few-flowered racemes, mark our species. The more important floral characters, however, were overlooked.

11. *Mitella japonica* (Sieb. et Zucc.) Miq. Ann. Mus. Bot. Lugd. Bat. III; 96. 1867. — *Mitellopsis japonica* Sieb. et Zucc. Fl. Jap. 1: 190. 1835 to 44. — Rhizome ascending, thickened; flowering stems erect, 2—4.5 dm. high, naked or sometimes with a single petioled leaf below the middle, hirsute and glandular-pubescent below, glandular-puberulent in the inflorescence; leaves cordate-ovate or ovate-oblong, 5—9-lobed, terminal lobe long-acuminate, doubly crenate-dentate, with mucronate-tipped teeth, hirsute with stiff scattered hairs above and along the veins beneath, 3.5—8 cm. long, 2.5 to 6 cm. wide; petioles slender, 5—15 cm. long, hirsute, with long retrorse

hairs and glandular-puberulent; raceme mostly secund, 10—27 flowered, 8—15 cm. long, becoming longer in age; bracts variously fringed or toothed; pedicels 1—2 mm. long, glandular-puberulent, mostly with 2 minute bracteoles at the base; flowers purplish, 6—7 mm. broad in anthesis; axis at first flattened but soon becoming turbinate; sepals broadly triangular, about 1 mm long spreading or ascending but not reflexed at the tips; petals pectinate-pinnatifid with 3—7 slender divisions, prominently glandular-dotted on the outside, 2.5—3.5 mm. long; stamens 5, inserted at the base of the petals, very short, anthers reniform; disk narrow, not prominently lobed; ovary nearly inferior, styles very short, stigmas mostly 4-lobed; dehiscing capsule turbinate, cup-shaped; seeds numerous, dark-spotted.

In moist woods, in the Islands of Kiusiu and Shikoku, Japan.

The species is somewhat variable in the size of the petals and in the number of their divisions. In the following variety much reduced petals are found:

Var. *integripetala* Makino, Bot. Mag. 49: 47. 1905. — »Leaves oval-ovate, deeply cordate with a close sinus, acute or sub-acute, shallowly lobate, with depressed-ovato-deltoid dentate lobes, very thinly pilose or sub-glabrous, dark green along the nerves, petals simple, subulato, filiform, smooth, recurved, reflexed, reddish above, stigma semi-orbicular, 2—4-lobulate, red.«

Flowers in April, Prov. Musashi: Tokio Cult. (T. MAKINO, May 9, 1904).

We have not seen this variety and the description is borrowed from Makino.

42. *Mitella acerina* Makino, Bot. Mag. 46: 459. 1902. — Rhizome erect or oblique, rooting stoloniferous; leaves tufted, long-petiolate, few-several, round cordate, usually acuminate, with a deep sub-closed sinus at the base, palmately 7-fid, lobes deltoid, or deltate-ovoid, membranaceous when dried, purple green, thinly pilose above, glabrous beneath, 5—9 cm. long, 5—8 cm. broad; petioles attaining 12 cm. in length; scapes few-several, erect, exceeding the leaves in height; glabrous below, shortly and sparsely glandular-hairy above, with several scaly bracts and sometimes bearing a small leaf towards the base; racemes densely and secundly many-flowered, glandular-hairy, attaining 40 cm. in length; pedicels equal to or shorter than the flowers; glandular-puberulent, bearing minute bracteoles at the base; bracts membranaceous, deltoid; flowers 9—10 mm. broad in anthesis; sepals deltoid, 4-nerved; petals 3.5—4 mm. long, 3-parted below the middle into linear lobes, glandular-dotted on the dorsal side, greenish purple; stamens 5, inserted at the base of the petals, filaments short, anthers cordate, rotund; disk thickish, flat on the surface; styles short, erect, stigmas thick, depressed oblong-semi-orbicular, very obscurely bi-lobed; ovary 4-celled, ovules numerous. (Description adapted from MAKINO, Bot. Mag. 1. c.).



Province of Wakasa: near Kumagawa (K. Tsuzi, April 10, 1904). Said to be a rare species, and to differ from *M. japonica* by the smaller and denser flowers, 3-fid petals, semi-glabrous leaves, glabrous petioles and sterile bracts upon the scape. Not seen by us.

### Part. III. Relationship and Geographical Distribution.

The accompanying diagram (fig. 9), seeks to show in a graphic way the relationship of the sections and species to each other and the course of evolution in the genus. Where 10 and 5-stamened species occur in a group of clearly related species like *Mitella*, the inevitable conclusion is that the forms with 10 stamens represent the older types and that those with

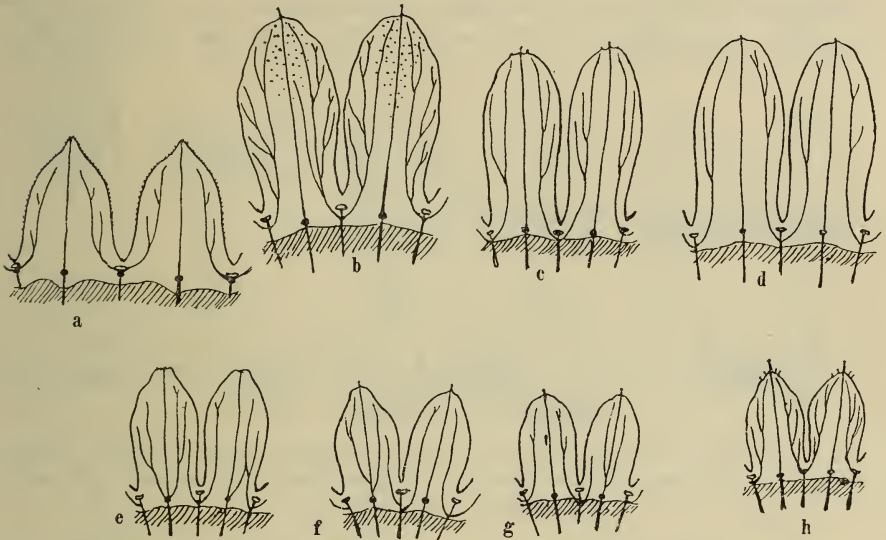


Fig. 1. Sepals in the Sect. *Eumitella*, showing venation, position of petals, stamens and disk. a *M. diphylla*, b *M. stauropetala*, c and d *M. stauropetala* var. *stenopetala*, e and f *M. trifida*, g *M. trifida* var. *violacea*, h *M. diversifolia*.  $\times 40$ .

5 stamens have been derived from them through reduction of one or the other of the two cycles of stamens. On this hypothesis, therefore, both *M. diphylla* and *M. nuda* are older types than the other species and form the starting points from which the others have evolved. These two parent forms show certain close similarities and also some very important divergencies of floral structure, as reference to the figures will show. For the sake of comparing these structures to the best advantage, drawings of the different organs of the flower of all the species except one, have been made and arranged in the sequence that we conceive the order of progression to have taken place. In this scheme the odd numbers of figures represent one series or section. The even numbers the other series or section.

It will be seen at a glance that what we might designate as the ground-plan of structure of each of the principal organs, namely, sepals, petals, stamens, pistil and axis, runs through all the species of each series in a remarkably consistent manner. In the odd numbered series the sepals are oblong in form, they are nearly erect in position, spreading only at the tips, freely veined, and white or violet-tinged in color (fig. 4). The petals show a progressive reduction from pinnately-cleft with numerous ascending divisions in *M. diphylla* through two diverging lines ending up in each case with reduced entire forms (fig. 3). They are white or violet-tinged in color. The stamens are short, sometimes nearly sessile; the anthers oblong, with slightly introrse dehiscence (fig. 5). The floral axis is distinctly cupshaped to begin with, and passes into campanulate or turbinate in the terminal representatives of the series. The pistil has an ovoid form,

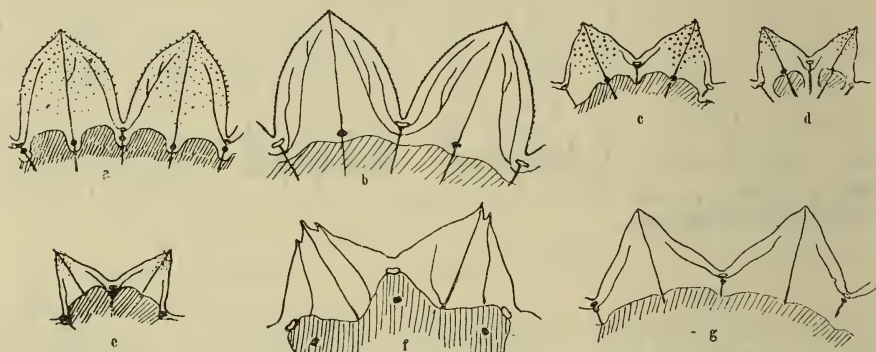


Fig. 2. Sepals in the Sect. *Mitellastra*, showing venation, position of petals, stamens and disk. a *M. nuda*, b *M. caulescens*, c *M. pentandra*, d *M. Breweri*, e *M. ovalis*, f *M. pauciflora*, g *M. japonica*.  $\times 40$ .

rather narrow to comply with the shape of the axis. The styles are very short, and are crowned by capitate or sometimes capitate-crescent-shaped stigmas (fig. 7).

In the even numbered series, the sepals are triangular or deltoid in form, they are widely spreading and often strongly reflexed at the tips, the veins are few, except in one large-sepaled species, and the color varies from greenish yellow to brownish (fig. 2). The plan of the petals is distinctly different from that in the other series. They are pectinate-pinnatifid, with narrow divisions that spread at right angles to the rachis. They range in color from greenish yellow to brownish purple and they vary from forms with many divisions to those with only the middle lobe remaining (fig. 4). The stamens run from distinctly filamented forms to almost sessile ones. The anthers vary from cordate to reniform, and the dehiscence from lateral to introrse (fig. 6). The floral axis is wide open saucer-shaped, and always much wider than deep. The pistil is shortened

and varies from almost spherical to short top-shaped, or much flattened. The styles vary from tapering cylindrical and ascending to clup-shaped and strongly spreading, but in no case do they bear any close resemblance

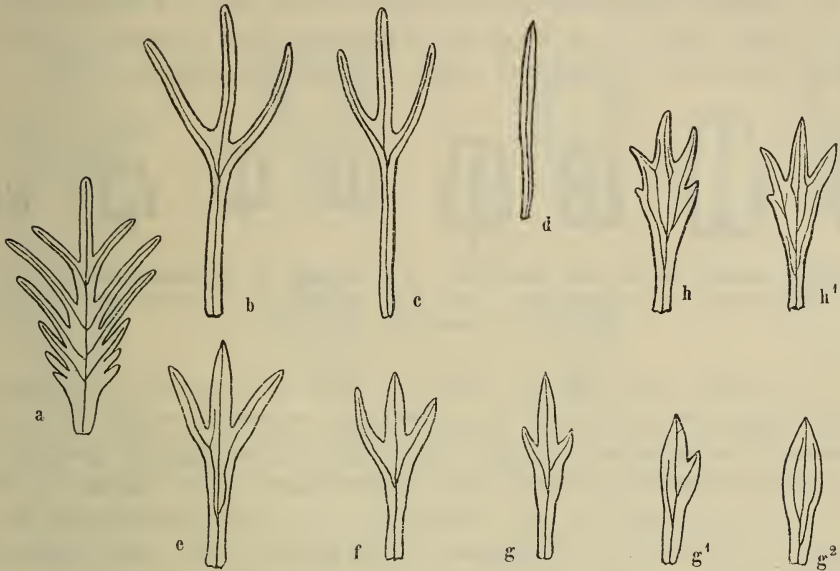


Fig. 3. Petals in the Sect. *Eumitella*. a *M. diphylla*, b *M. stauropetala*, c and d *M. stauropetala* var. *stenopetala*, e and f *M. trifida*, g, g<sup>1</sup> and g<sup>2</sup> *M. trifida* var. *violacea*, h and h<sup>1</sup> *M. diversifolia*.  $\times 40$ .

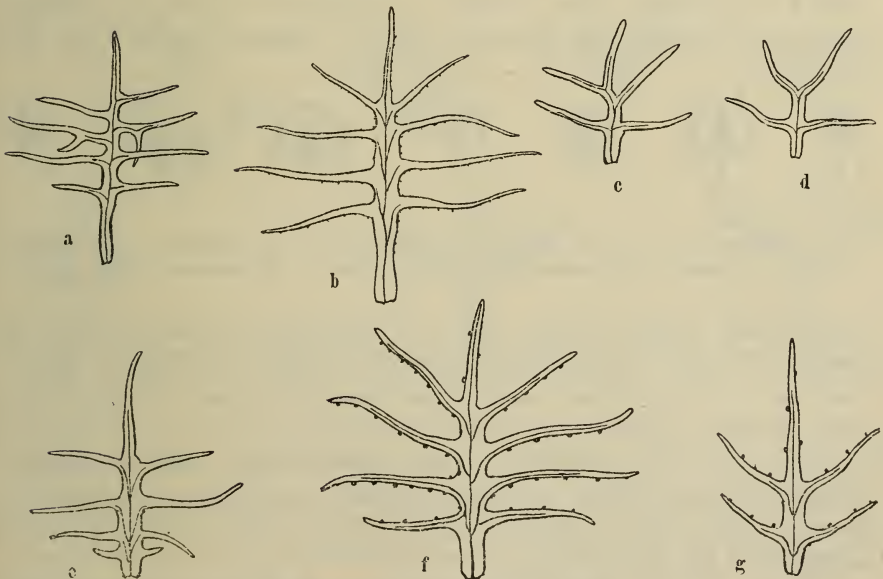


Fig. 4. Petals in the Sect. *Mitellastra*. a *M. nuda*, b *M. caulescens*, c *M. Breweri*, d *M. ovalis*, e *M. pentandra*, f *M. pauciflora*, g *M. japonica*.  $\times 40$ .



to those in the other series. The stigmas are either small, entire and pointed or else more or less prominently 2—4-lobed (fig. 8).

To these characters should also be added the one of short, thick, nearly always ebracteolate flower-pedicels of the section *Eumitella*, and the slender, more or less elongated, bi-bracteolate flower-pedicels and frequent occurrence of 2-flowered cymes of the section *Mitellastra*.

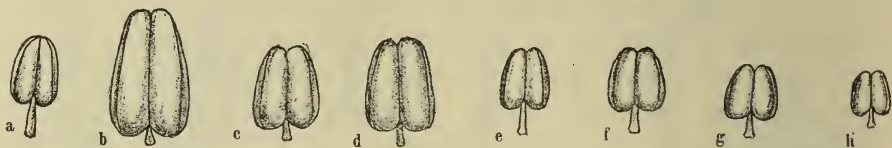


Fig. 5. Stamens in the Sect. *Eumitella*. a *M. diphylla*, b *M. stauropetala*, c and d *M. stauropetala* var. *stenopetala*, e and f *M. trifida*, g *M. trifida* var. *violacea*, h *M. diversifolia*.  $\times 10$ .

It would seem from all this that when as many as four distinct floral structures coincide in the remarkable manner in which they are shown to do in these two series, there can be no doubt about the genetic development following the two main lines indicated in our diagram (fig. 9). It is on the ground of the combination of so many fundamental characters as this that a new alignment of the species of the genus *Mitella* is proposed. As already pointed out, the division of the genus has been made purely upon the number and position of the stamens, with the result that the sections have run squarely across the lines of genetic development instead of paralleling them. There are, therefore, not only no adequate reasons for dividing the genus up into five distinct sections, but such

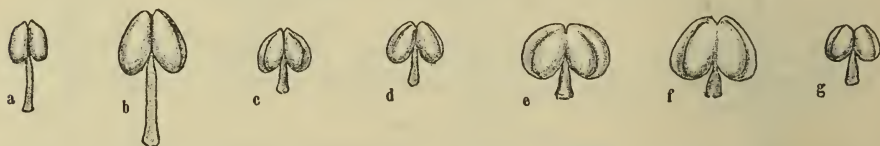


Fig. 6. Stamens in the Sect. *Mitellastra*. a *M. nuda*, b *M. caulescens*, c *M. Breweri*: d *M. ovalis*, e *M. pentandra*, f *M. pauciflora*, g *M. japonica*.  $\times 10$ .

divisions also violate or ignore the true relationship existing between the species. To us it appears most natural to regard *M. diphylla* und *M. nuda* as two present-day basic types that have already diverged from some common ancestral type which has disappeared. They are about on the same level of development. They approach each other in structure of the floral axis and in the stamen number, but in other respects they diverge. From them as starting points have been developed in connected sequence all the living species.

In one direction *M. diphylla* has given rise to the *M. trifida* group in about the following manner. A deepening of the floral axis has taken

place and a consequent greater fusion of the ovary with it, a reduction of the stamen number to the 5 episepalous ones on account of the closer crowding due to the narrowing of the axis, a progressive reduction of the divisions of the petal from the base upward, leaving only the last

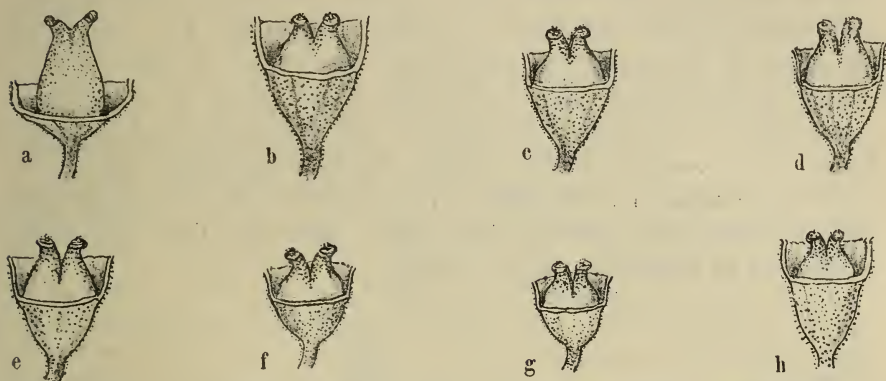


Fig. 7. Pistils in the Sect. *Eumitella*, showing shape and extent of fusion with the axis. *a* *M. diphylla*, *b* *M. stauropetala*, *c* and *d* *M. stauropetala* var. *stenopetala*, *e* and *f* *M. trifida*, *g* *M. trifida* var. *violacea*, *h* *M. diversifolia*.  $\times 10$ .

one on each side, and finally in Var. *violacea* a disappearance of all the divisions of the petal leaving only the middle portion. This reduction of the petals has followed hand in hand with the reduction of the size of the rest of the flower. An exactly similar course can be traced in the

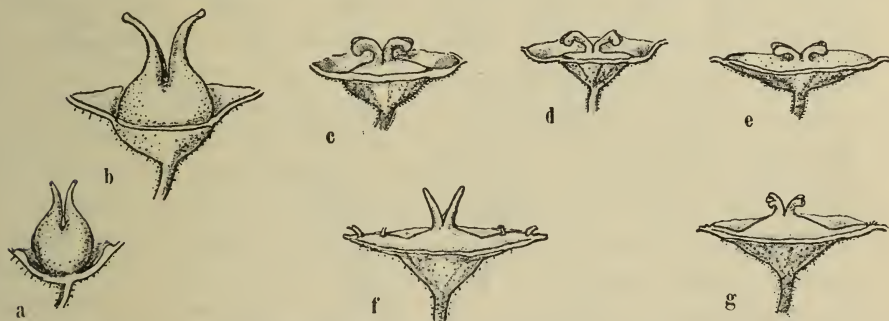


Fig. 8. Pistils in the Sect. *Mitellastra*, showing shape and extent of fusion with the axis. *a* *M. nuda*, *b* *M. caulescens*, *c* *M. Breweri*, *d* *M. ovalis*, *e* *M. pentandra*, *f* *M. pauciflora*, *g* *M. japonica*.  $\times 10$ .

*M. stauropetala* group, ending up in a similar manner in small entire petals in individuals of Var. *stenopetala*. Somewhat more divergent is *M. diversifolia* with many-veined, 3—5-cleft petals, but all the other floral structures show unmistakable connections with *M. trifida* and the species has undoubtedly arisen from this branch.

Turning to the other Section of which *M. nuda* is the origin, we

find slightly more diversity but no less distinct continuities of development. In this section, three distinct lines are evident. The middle line, represented by *M. caulescens*, is a direct continuation of *M. nuda* differing essentially from the basic type only in having 5 episepalous stamens, and in the slightly larger size of all its parts. The close relationship indicated by the floral characters is further strengthened by a very close agreement in the anatomy of the rhizome and scape. In both species a distinct endodermis surrounds the vascular tissue system of the rhizome. The extent and structure of the cortex is almost indential and the distribution of the vascular bundles and the ring of strengthening cells in the scape is the same in both species. These facts are the more noteworthy because all the other species of the genus differ from these two in the absence of an endodermis in the rhizome.

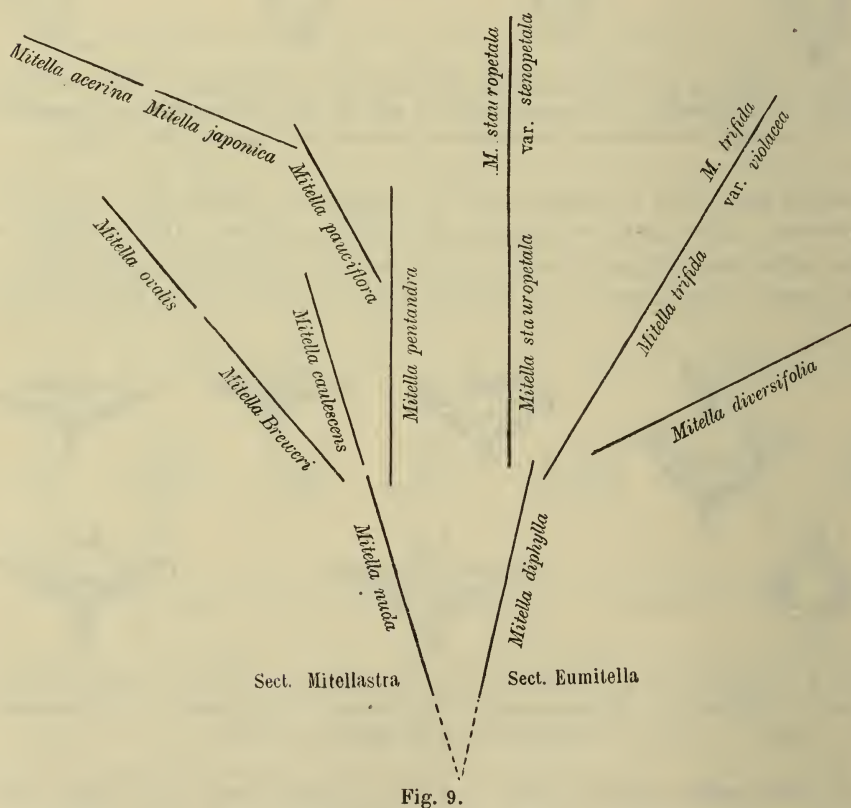


Fig. 9.

The two other branches of the section have diverged separately from the basic type. The species of both these branches have the reduced stamen number, but as one series has retained the episepalous stamens and the other the epipetalous ones, it is clear that they trace separately



to a 10-stamened ancestor. There is the possibility that the *M. Breweri-M. ovalis* line could have arisen from *M. caulescens* but it seems more reasonable to assume that the origin would have to be looked for in the more general basic region than in the more specialized terminal one.

The same tendency towards the reduction of the size of the flower, the sinking of the ovary deeper into the hollow axis and the reduction in the number of divisions of the petals that obtained in the other section, characterize both these branches. *M. ovalis* of the *M. Breweri* branch has a completely inferior ovary and the petals have from 6 to 3 divisions. It marks the termination of this line of development.

The *M. Pentandra* branch is characterized by having the stamens placed opposite the petals and by the development of a prominent disk which more or less covers the top of the ovary. This branch is perhaps not as direct a series as our diagram would indicate, for it is probable that *M. pauciflora* and *M. japonica* diverge from a nearly common starting point. The terminal representatives in any case would be *M. acerina* with petals with 3 divisions, and *M. japonica*, var. *integripetala*, with slender, entire petals.

A consideration of the geographical distribution of the various species throws considerable additional light upon their relationship and a reference to the accompanying chart will help to bring this out.

The primary centre of development of the genus lies in the mountain region of southern British Columbia, western Montana, Idaho, Washington, Oregon and northern California. A secondary centre has developed in southern Japan. As far as present distribution can throw light on what has gone before it seems most probable that the genus originated in Alaska and that in Tertiary times it must have extended northward to beyond the barrier of the Rocky Mountains. From the Alaskan place of origin it spread out or wandered in three directions. The two oldest species *M. diphylla* and *M. nuda* migrated southeastward through the forest country of Canada in preglacial times as far as the Atlantic ocean. The present isolation of *M. diphylla* in eastern North America must be ascribed to the glacial period. This species, being adapted to temperate climates and low altitudes has subsequently not been able to penetrate farther northward again than to about the 47° parallel of latitude. Furthermore being a woodland species its westward progress has been determined by the limit of the deciduous forests.

The North American distribution of *M. nuda* practically co-incides with the geographical area of *Picea canadensis*. In Asia it extends westward as far as the Yenisei River and south to the latitude of Lake Baikal. The wide geographical range of this species is the more remarkable when it is borne in mind that it has no special contrivances for seed distribution; and it would indicate that the species is of great age.

The two main stocks of the genus which developed in the area of origin also began moving southward in the mountains during pre-glacial times and in their progress soon evolved several new species.

The *M. Breweri* — *M. ovalis* group branched off early and attained the greatest southward range of the west American species. Of these two *M. Breweri* is much the older judging both by its greater geographical distribution and by the greater number of variations or divergences from the type. On the various outposts of its range several more or less distinct forms can be differentiated, but these have as yet not diverged far enough to be regarded as species or even as good varieties.

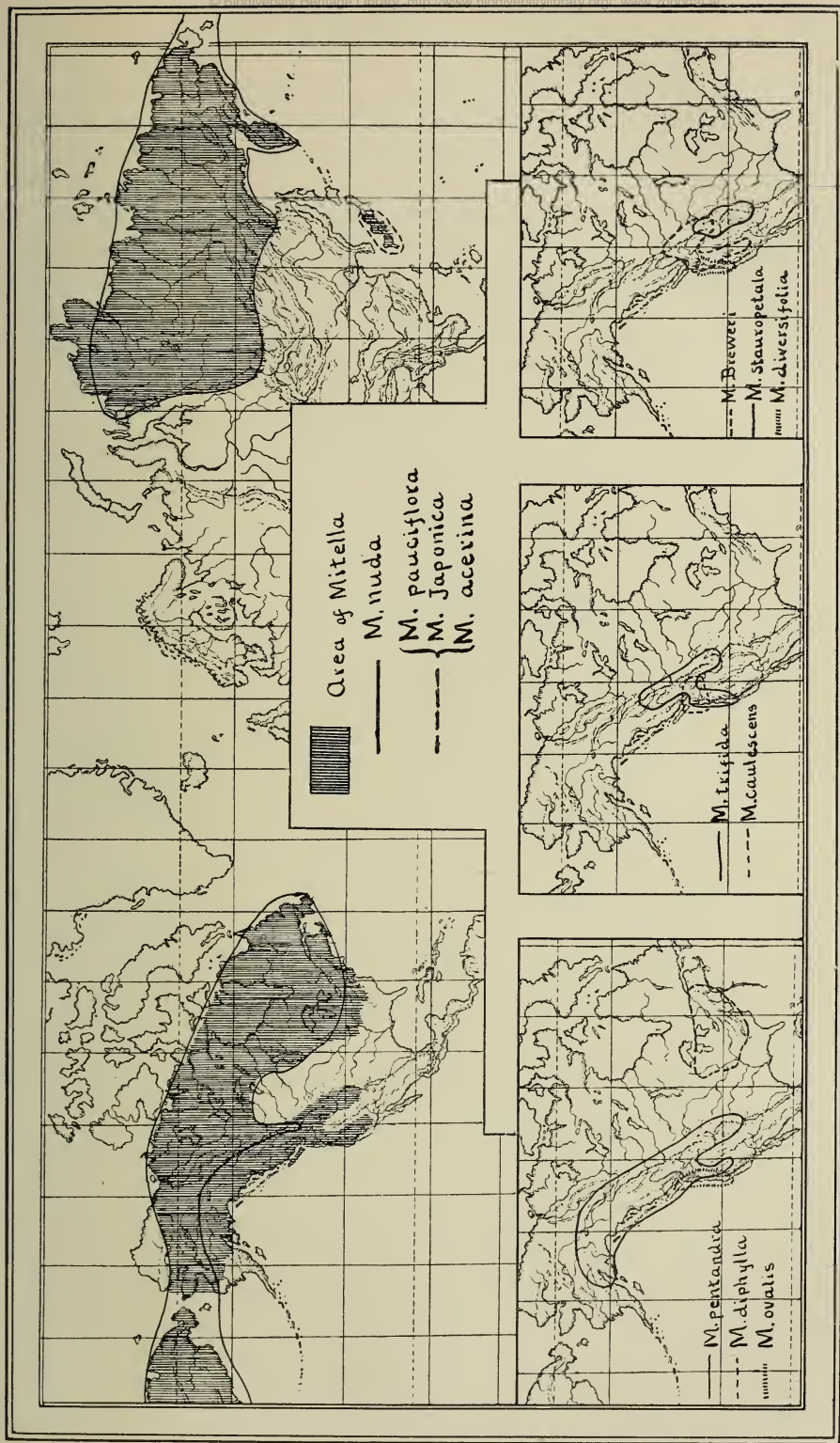
The relationship of *M. ovalis* with *M. Breweri* is so obvious and unmistakable that there is no possible doubt as to its origin. It represents the lowland extension of the alpine ancestor. Its distribution is confined to a comparatively narrow strip of the Pacific coast from northern California to Vancouver Island and it is undoubtedly one of the youngest of all the species.

The *M. pentandra* group probably arose within the original centre and the species has spread far southward to southern Colorado in the Rocky Mountains and nearly to middle California in the Coast, Cascade and Sierra Nevada Mountains. It is more uniform than many of the other species and it is only on the isolated high mountains like Mt. Ranier that occasionally diverging forms appear. From this stock a branch diverged early and spread westward across to eastern Asia and wandered southward to Japan. It has subsequently become isolated in the southern half of the Island Empire and has developed into three clearly related yet well marked species.

The most direct phylogenetic line is the one leading from *M. nuda* to *M. caulescens*. It is probable that the latter species originated very close to or probably within the area that it occupies today. Its somewhat limited distribution would indicate a comparatively recent origin.

The species evolved from the *M. diphylla* stock have held more to the eastern parts of the Rockies than those developed from the *M. nuda* stock although a branch has extended westward into the Cascade and Coast ranges.

*M. trifida* is probably the oldest of the species in this relationship and is one of the most polymorphous of the whole genus. Numerous forms could be differentiated and it is evident that the species is still in a very active state of evolution. Variety *violacea* forms the southward extension of the species in the Rocky Mountains of Montana and appears fairly constant. It occurs northward in British Columbia with the species. *M. stauropetala* is more southern in its range and seems to represent the termination of the stock in this direction. It runs through the correspon-







ding variations of *M. trifida* and is nearly as polymorphous. It ranges from northern to southern Idaho and by successive degrees in reduction of the flower parts, it becomes in northern Utah, in Wyoming and Colorado the var. *stenopetala*.

*M. diversifolia* stands somewhat apart both in its curious leaves and petals but connects undoubtedly with *M. trifida* stock. It seems to have diverged from the Cascade Mountain branch of *M. trifida* in comparatively recent times and has spread only from southern Washington to northern California.